

**LIFE HISTORY AND SYSTEMATICS OF THE
WEST ANDEAN MOTH *AUCULA FRANCLEMONTI* WITH
DESCRIPTION OF A NEW SPECIES FROM ECUADOR
(LEPIDOPTERA: NOCTUIDAE: AGARISTINAE)**

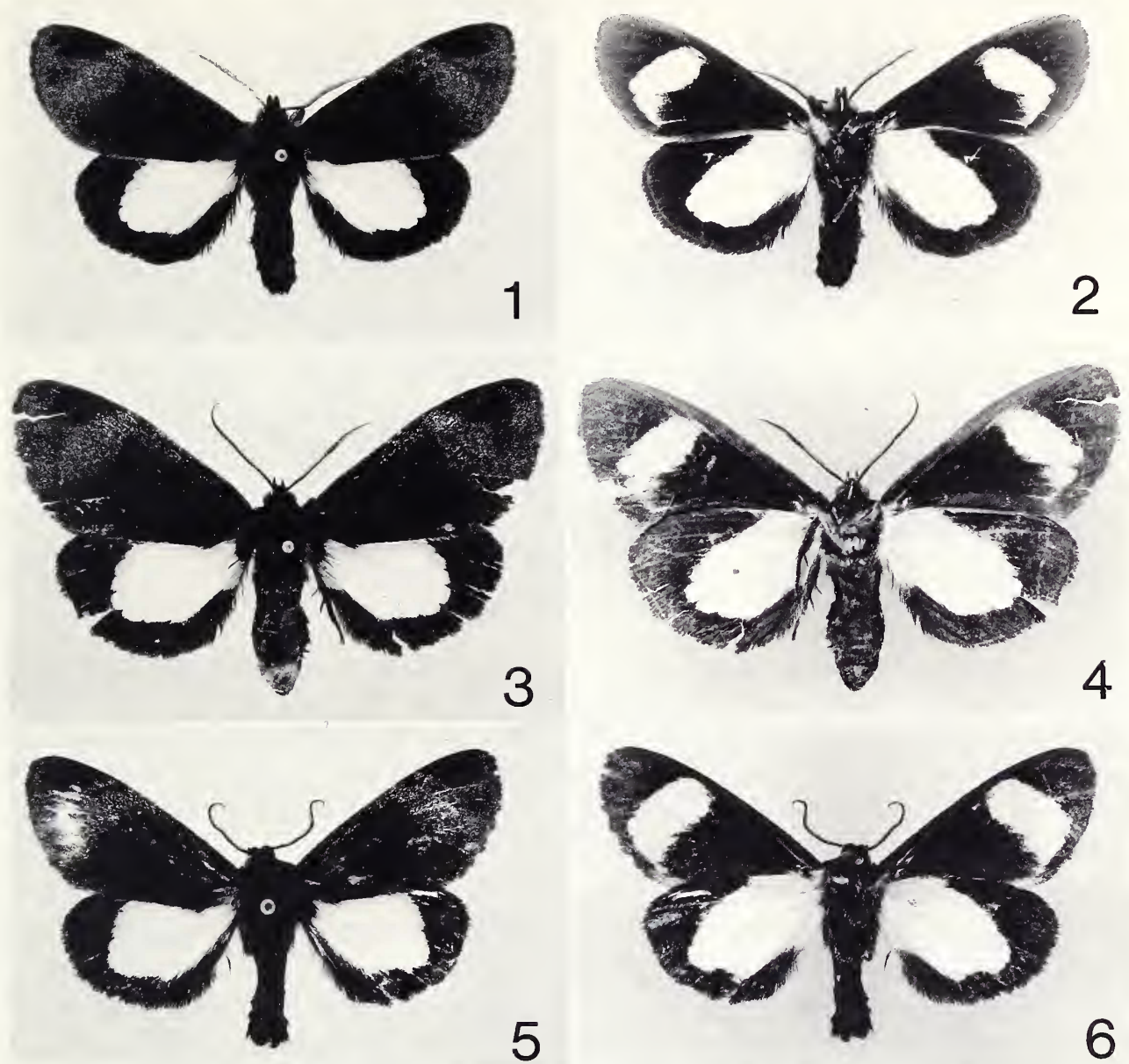
JOHN E. RAWLINS

Section of Invertebrate Zoology, Carnegie Museum of Natural History,
4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213

Abstract.—Systematics, biology, and morphology of the rare South American agaristine moth, *Aucula franclemonti* Todd and Poole (Lepidoptera: Noctuidae), are presented in the context of other agaristine genera. *A. kimsa* Todd and Poole is placed in synonymy with *A. franclemonti*, and *A. ivia* Todd and Poole is synonymized with *A. tusora* Todd and Poole; *A. franclemontoides*, new species, is described from east Andean Ecuador. A brief phylogenetic analysis of the five species in the *A. franclemonti* species-group is offered, with a key to the species-group based on male genitalia. Female genitalia of *A. franclemonti* are described, and an external mating plug (sphragis) noted, perhaps functionally related to a permanently everted and sclerotized endophallus in males. Larvae were found feeding on *Vitis tiliifolia* Humb. & Bonpl. (Vitaceae), and all immature stages reared from the egg are briefly described. A complete chaetotaxy of the last instar larva is illustrated in detail. Modifications of the pupal cremaster and the presence of subventral seta SV2 on the seventh abdominal segment are apomorphic features shared only with other agaristine species.

Species of *Aucula* are infrequently encountered agaristine moths found in semiarid to mesic habitats in Panama and tropical South America. Kiriakoff (1977) summarized the taxonomic status of species described by earlier workers. In 1981, Todd and Poole revised *Aucula*, thoroughly describing adult males and providing a key to all species based on the male genitalia. They recognized as valid three previously described species, transferred two species to related monobasic genera (*Arpia* Schaus and *Darcetina* Felder), and excluded three species from *Aucula*, leaving them temporarily in generic combinations as originally described. They also described 21 new species based primarily on genitalic differences after examining slightly more than 100 male specimens in the following collections: National Museum of Natural History, Washington, D.C. (NMNH); The Natural History Museum, London (BMNH); Universidad Central de Venezuela; Zoologische Sammlung des Bayerischen Staates, Munich; and Carnegie Museum of Natural History, Pittsburgh (CMNH). Of the 24 species currently considered valid (Poole, 1989), nine are known from unique types, and only seven species are known from more than five specimens. The longest series for any species is 18 specimens (*Aucula ivia* Todd and Poole), 13 of which are from the same locality. Todd and Poole mentioned only 12 female specimens associated with six species but did not figure adult females or their genitalia.

A series of 23 males and two females of *A. franclemonti* Todd and Poole were collected at a single locality in western Ecuador during the summer of 1983. *A. franclemonti* was previously known only from the holotype. This material constitutes the largest known series of any *Aucula* species, providing information on character

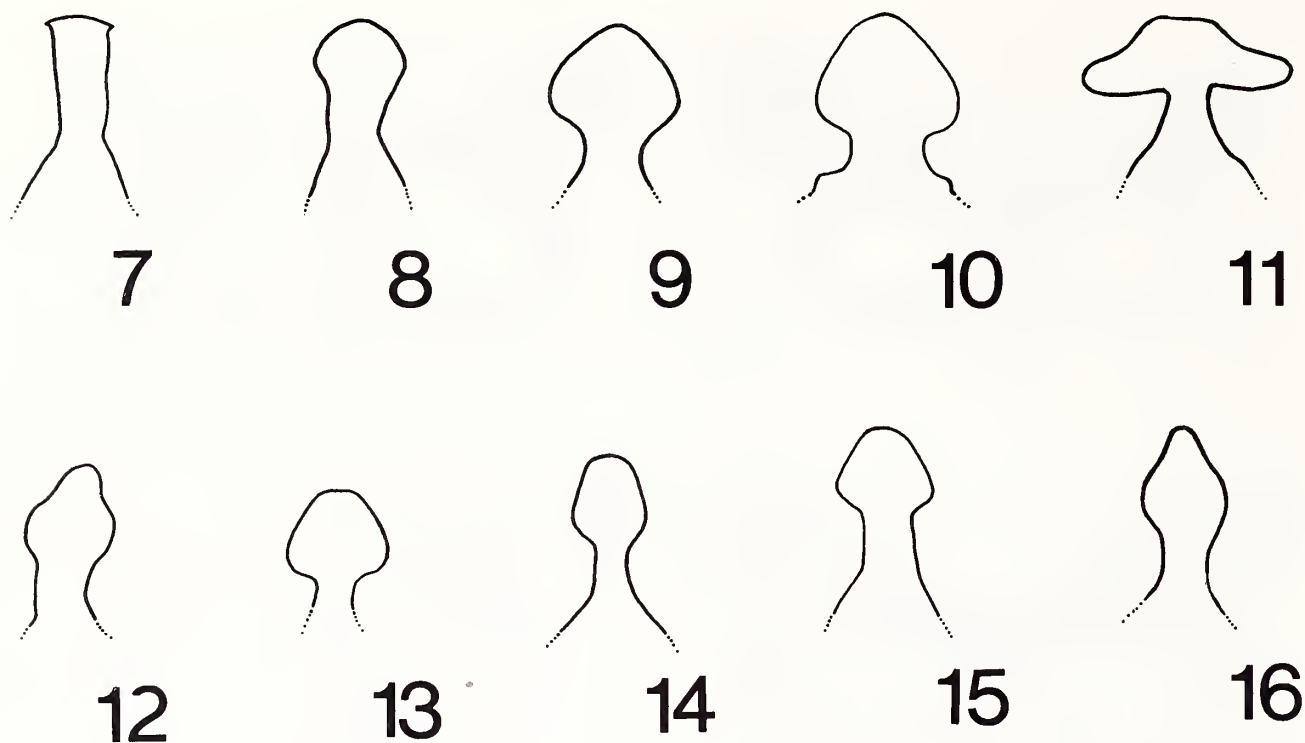


Figs. 1–6. Adults of *Aucula*, dorsal (left) and ventral views (right). 1–2. *A. franclemonti*, male; forewing length 25 mm; Ecuador, Carchi (CMNH). 3–4. *A. franclemonti*, female; forewing length 27 mm; Ecuador, Carchi (CMNH). 5–6. *A. franclemontoides*, holotype male; forewing length 24 mm; Ecuador, Morona-Santiago (CMNH).

variation not available to Todd and Poole. Eggs were also obtained and the immature stages reared; a larva was found feeding in the field and an adult female was reared from it, confirming the identity of the foodplant. The following paper reviews the systematics of *A. franclemonti* and closely related species, describes as new a related species from eastern Ecuador, describes the female genitalia, provides basic life history information, and presents a detailed morphological description of the larva in the context of other agaristine and noctuid larvae.

SYSTEMATICS OF THE *AUCULA FRANCLEMONTI* GROUP

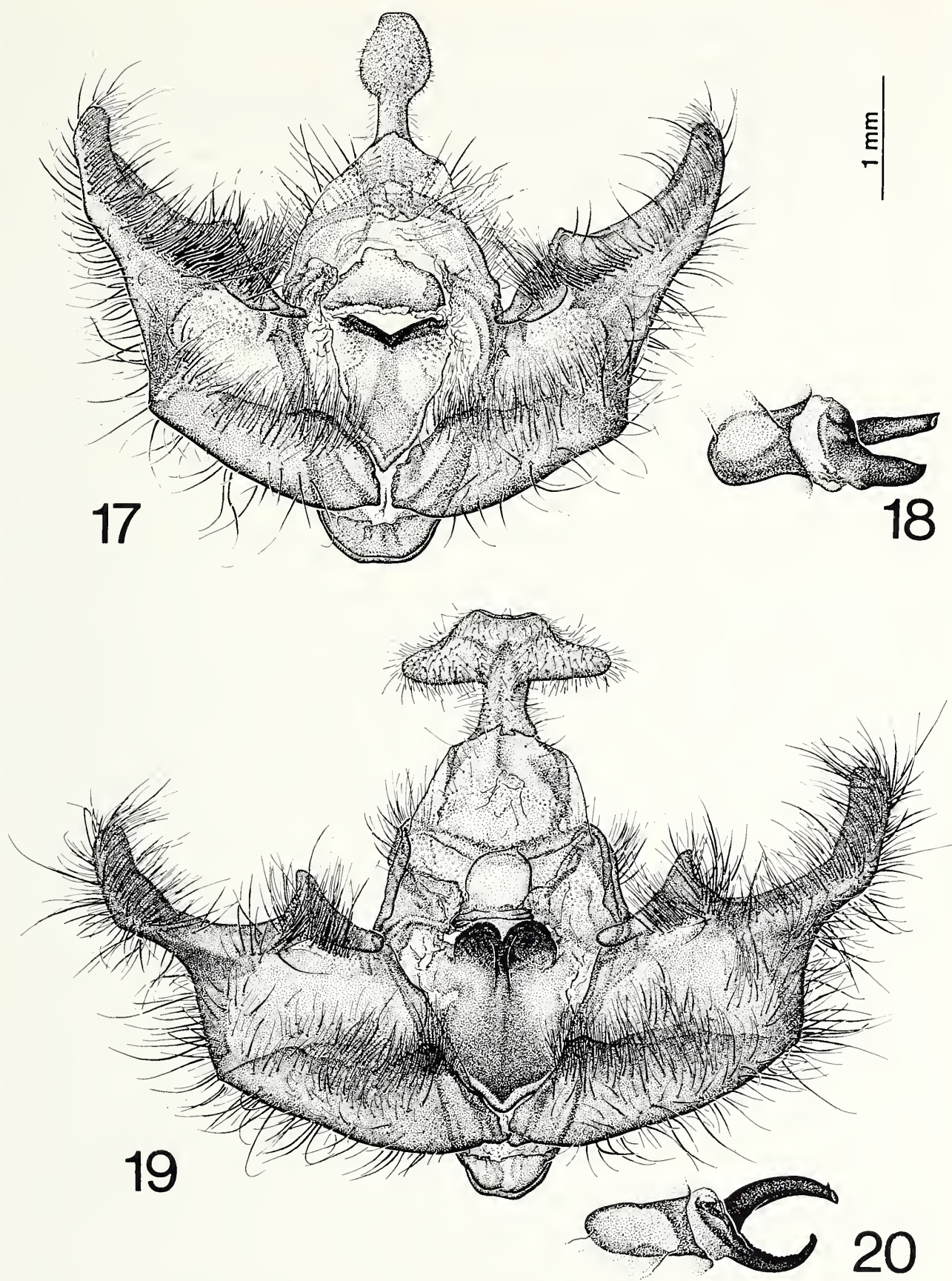
Todd and Poole (1981) informally recognized a group of six superficially identical species of *Aucula* from the Andes “characterized by an enlarged broad uncus and a



Figs. 7–16. Outlines of uncus from male genitalia of species in the *Aucula franclemonti* group (Figs. 7–10 and 12–13 taken from Todd and Poole (1981)). 7. *A. jenia*, holotype. 8. *A. otasa*, holotype. 9. *A. tusora*, holotype. 10. *A. ivia*, holotype. 11. *A. franclemontoides*, holotype (Genitalia slide: Rawlins 860 (CMNH)). 12. *A. kimsa*, holotype. 13. *A. franclemonti*, holotype. 14. *A. franclemonti* (Genitalia slide: Rawlins 849 (CMNH)). 15. *A. franclemonti* (Genitalia slide: Rawlins 858 (CMNH)). 16. *A. franclemonti* (Genitalia slide: Rawlins 857 (CMNH)).

characteristically shaped valve,” the latter referring to the abruptly angled ventral margin at the distal end of the sacculus and a slender, setose, and smoothly arched valve apex. These genitalic features are unique to this group, both in the context of other species in the genus, as well as other species of Agaristinae (Kiriakoff, 1977). Their apomorphic condition supports the monophyly of a taxon here christened the *A. franclemonti* group. All specimens in this group examined by Todd and Poole were from Colombia and Ecuador west of the Andes, or from southern Peru and adjacent Bolivia east of the Andes.

Todd and Poole (1981) described the largest individuals in the group (FWL = 26–27 mm) as two species, *A. franclemonti* based on a single male (NMNH), and *A. kimsa* based on two males (BMNH). All type specimens of both species are from the same locality in western Colombia, San Antonio near Cali. The two species were distinguished by the shape of the distal half of the uncus, smoothly lobed in *A. franclemonti* (Fig. 13) and contrastingly concave in *A. kimsa* (Fig. 12). Similarly, Todd and Poole (1981) described two medium-sized species (FWL = 19–22) from northwestern Bolivia and adjacent southeastern Peru, *A. ivia* based on 18 males from both countries (NMNH, BMNH, CMNH), and *A. tusora* based on a single male from Bolivia. *A. tusora* was distinguished from *A. ivia* by the smoothly tapered base of the uncus, contrasting with a distinctive, angulate, or “shouldered” condition in *A. ivia*. Other than this condition, the habitus and male genitalia of the two species are virtually identical despite the somewhat worn condition of the unique type specimen of *A. tusora*.



Figs. 17–20. Male genitalia of *Aucula*. 17. External genitalia of *Aucula franclemonti* (Genitalia slide: Rawlins 848 (CMNH)). 18. Aedeagus of *Aucula franclemonti* (Genitalia slide: Rawlins 849 (CMNH)). 19. External genitalia of male holotype of *Aucula franclemontoides* (Genitalia slide: Rawlins 860 (CMNH)). 20. Aedeagus of male holotype of *Aucula franclemontoides*.

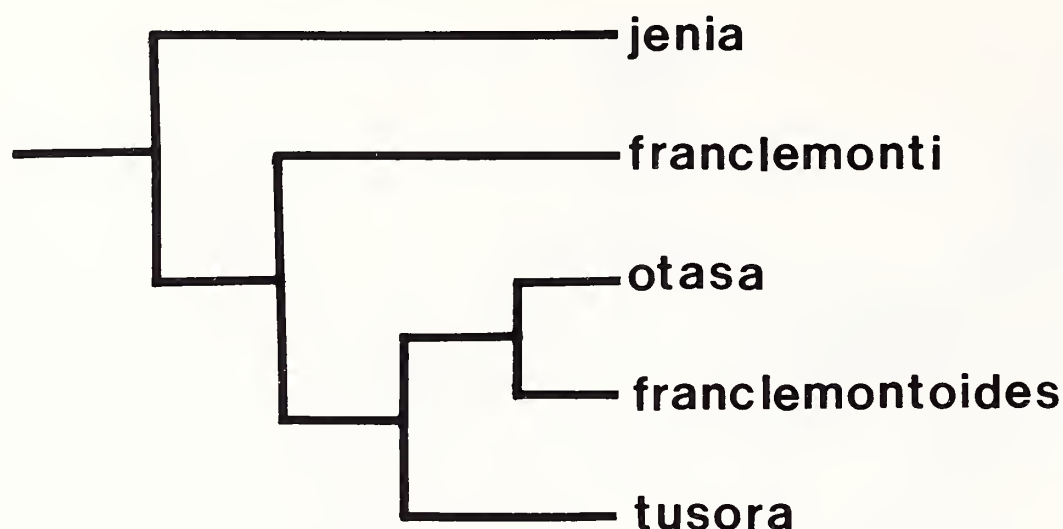


Fig. 21. Hypothesized phylogenetic relationship among species in the *Aucula franclemonti* species-group.

The *A. franclemonti* species-group contains two other distinctive and easily recognized species. The smallest in the group (length of forewing, FWL = 17 mm), *A. otasa* Todd and Poole, was described from a single Bolivian male (BMNH) and characterized by an autapomorphic incision of the dorsal margin of the sacculus, a very sharply angled emargination of the ventral outline of the valve apex distal to the saccular angulation, and a spatulate uncus (Fig. 8). Another medium-sized species from western Ecuador, *A. jenia* Todd and Poole (FWL = 23–24 mm), is easily recognized by an unique black bar across the yellow basal region on the ventral side of the hindwing (Fig. 25), and by male genitalia with a nearly straight outer margin beyond the saccular angulation and a broadened, strap-like uncus without lateral lobes (Fig. 7). The black wing bar is autapomorphic for *A. jenia*, but the genitalic features are considered plesiomorphic as for most species of *Aucula* other than those in the *A. franclemonti* group. One additional specimen of *A. jenia* has been examined and found to agree with all diagnostic features of the type series (Ecuador, Chimborazo, 11 km NE Pallatanga, 2,800 m, 11 November 1987, C. Young, R. Davidson, J. Rawlins (CMNH)).

Capture of 23 males in the *A. franclemonti* group at a single locality in northwestern Ecuador near the Colombian border (Ecuador, Carchi, Chical, 00°56'N, 78°11'W, 1,250 m, J. Rawlins, R. Davidson (CMNH)) provide new data on the nature and extent of variation in adult characters, including those purportedly diagnostic for *A. franclemonti* and *A. kimsa*. Specimens were taken during a period of intensive collecting extending from June 21 to August 16, 1983, and include the following dates (number of male specimens in parentheses): June 29 (1), July 1 (2), July 2 (6), July 5 (1), July 6 (1), July 8 (1), July 11 (3), July 15 (1), July 17 (4), July 18 (1), August 1 (1), August 7 (1). All genitalic features were assessed in six males by dissection, and the shape of the uncus and the distal half of the valve was examined in all remaining males by brushing abdominal apices.

All males were virtually identical in color and wing pattern (Figs. 1–2). There is slight variation in forewing size: FWL, 23–27 mm; mean = 24.8 mm; mode = 25 mm; N = 23. Several genitalic features are highly variable, especially the degree of setation and sclerotization of the valves and the shape and degree of sclerotization

of the uncus. In particular, the shape of the distal half of the uncus varies from a condition more deeply concave than that of the type specimen of *A. kimsa* to individuals with lateral lobes larger than those on the type specimen of *A. franclemonti* (Figs. 12–17). Collection of these specimens at a single locality over a short time period suggests they are conspecific members of a single population exhibiting considerable intrapopulation variation in genitalic characters, especially the shape of the uncus. Type specimens of *A. kimsa* and *A. franclemonti* fall within the range of character variation observed in this series, and their recognition as separate species is not supported. In contrast, some features of the male genitalia do not vary, notably the shape and sclerotization of the juxta, and the shape and size of the aedeagus (see discussion below).

The degree and extent of sclerotization at the base of the uncus in this conspecific series of *A. franclemonti* also varies greatly, ranging from a weakly sclerotized condition with smoothly arched outline to a more strongly sclerotized condition resulting in angled “shoulders” at the uncus base. The latter condition is very similar to the only diagnostic feature separating the single male type of *A. tusora* from the relatively extensive series of *A. ivia*, suggesting, albeit indirectly, that those two names represent but a single species as well.

In addition to the above specimens from western Ecuador, a single, slightly damaged specimen of *Aucula* was captured in Ecuador in a wet forest on the eastern slope of the Andes. Because this specimen was the first *Aucula* specimen known to me from the eastern Andean region north of southern Peru, special attention was given to its study. Externally the specimen closely resembles *A. franclemonti* and *A. tusora* (Fig. 3), but genitalic dissection revealed a distinctive new species of *Aucula* of the *A. franclemonti* group (Figs. 19–20).

***Aucula franclemontoides*, new species**

Figs. 3–4, 19–20

DIAGNOSIS. This tropical American species is placed in the genus *Aucula* by the following combination of characters: rounded (not falcate) forewings, characteristic wing pattern (Fig. 3–4), lack of a yellow basal patch on the ventral side of the forewing, and male genitalia lacking a distinct median process on the sacculus. It differs from all described species of *Aucula* by features of the male genitalia, especially the strongly sclerotized, enlarged lobes on the dorsal margin of the juxta and the greatly enlarged and elongated lateral lobes of the uncus (Fig. 19).

DESCRIPTION (male only, female unknown). Forewing: length, 24 mm; maximum width, 12 mm. Hindwing: length, 18 mm. Extremely similar in all external features to *A. franclemonti* Todd and Poole, including antennal pectination, shape and size of frontal process, color pattern of wings and body; differs from *A. franclemonti* as follows: ground color of forewing brownish black, slightly darker and less reddish brown than *A. franclemonti* and similar in color to *A. jenia*; outer margin of yellow basal patch on hindwing smoothly and evenly curved as in *A. tusora* and *A. otasa*, not crenulate due to faint inward extension of black scales along veins as in *A. franclemonti* and *A. jenia*.

Male abdomen. Abdominal terga 3–7 with antecostae evanescent on midline; Ter-

gum 8 subquadrate, unmodified; Sternum 8 with anterior margin slightly thickened and sinuate. Abdominal Segment 2 with lateral hair pencils resting in scale-lined, elongate pleural invaginations on segments 2–4.

Male genitalia. Figures 19–20. Tegumen slightly wider than long, strongly sclerotized dorsally, membranous ventrally. Vinculum narrow; saccus not developed. Juxta a smooth flattened plate, subacute ventrally, prolonged dorsally into two rounded and posteriorly extended lobes separated by a deep notch; lobes of juxta heavily sclerotized, densely covered with microscopic spinules. Anellifer membranous except in region immediately adjacent to aedeagus. Uncus inflated at base to more than half width of tegumen, narrowly constricted at middle, then abruptly dilated into two long lateral lobes and terminated in a very short, broadly truncated, and slightly asymmetrical apex. Valves symmetrical, subtrapezoidal, with elongate, curved apices; costa with large triangular process at middle subtended by flat, coarsely setose editum; sacculus broad, setose, with ventral margin smoothly curved, forming abrupt obtuse angle with apex of valve; dorsal margin of sacculus distinct, raised into rounded prominence near base of valve; apex of valve constricted distally with outline strongly concave ventrally and dorsally; valve with distal end slightly flattened and widened, dorsally deflected, and densely setose on mesal surface.

Aedeagus greatly modified (Fig. 20); basiphallus broadly expanded anteriorly into a weakly sclerotized coecum; distiphallus shorter than its diameter, but bearing dorsally a strongly sclerotized, flattened, apical process which curves smoothly ventrad; endophallus (vesica) permanently everted, very heavily sclerotized, forming a hollow tube curved dorsad, terminated in a subcircular meatus (primary gonopore) with a minute spinule approximate to its ventral lip.

BIOLOGY AND IMMATURE STAGES. Unknown, but are expected to be very similar to those of *A. franclemonti*, described below. Expected foodplants for *A. franclemontoides* and other species of *Aucula* are species of *Vitis* and related genera of Vitaceae.

DISTRIBUTION. Known only from the type locality where the habitat is submontane rainforest of exceptional richness and floristic diversity.

DISCUSSION. Diagnostic modifications of the juxta and uncus leave little doubt that this species is distinct from other members of the *A. franclemonti* group.

Of special interest is the aedeagus, which is similar to those of other species in the *A. franclemonti* group, none of which was figured by Todd and Poole (1981). They interpreted the aedeagus to have a “vesica without spines or cornuti,” but careful study and dismemberment of one aedeagus did not reveal any eversible structure beyond the external meatus of the strongly sclerotized, tubelike apex of the phallus. Comparative study of the aedeagus reveals that the basiphallus (portion of aedeagus internal to junction with anellus (manica)) is inflated and weakly sclerotized. The distiphallus (sclerotized external portion of aedeagus from manica to base of endophallus) is very short with an elongate dorsal process. The endophallus is not membranous, but rather very strongly sclerotized into a permanently everted tube so that the apparent apical opening of the phallus is the primary gonopore, not the secondary gonopore (phallotreme) as is the usual case in most Lepidoptera.

PRIMARY TYPE DATA. Holotype male, CMNH. Verbatim text of four pin labels: ECUADOR: Morona-Santiago. Rio Culebrillas, 34 km SE Gualaceo. 2,200 m. 22–23 Oct 1987 / J. Rawlins, C. Young, R. Davidson. Wet forest. / Genitalia

Slide No. 860 John E. Rawlins / HOLOTYPE *Aucula franclemontoides* Rawlins [red paper].

Etymology: The name *franclemontoides* is an adjective referring to the great resemblance of this species to *A. franclemonti*.

ALPHABETICAL CHECKLIST OF SPECIES IN THE *AUCULA FRANCLEMONTI* GROUP

- Aucula franclemonti* Todd and Poole, 1981.
- Aucula kimsa* Todd and Poole, 1981. **NEW SYNONYMY.**
- Aucula franclemontoides* Rawlins, new species.
- Aucula jenia* Todd and Poole, 1981.
- Aucula otasa* Todd and Poole, 1981.
- Aucula tusora* Todd and Poole, 1981.
- Aucula ivia* Todd and Poole, 1981. **NEW SYNONYMY.**

KEY TO ADULTS OF SPECIES IN THE *AUCULA FRANCLEMONTI* GROUP
BASED PRIMARILY ON THE MALE GENITALIA
(Derived in part from key in Todd and Poole, 1981)

- 1. Uncus widest near middle (Figs. 8–17, 19); yellow region on lower surface of HW unmarked (Figs. 2, 4, 6) 2
- Uncus widest at apex, strap-like (Fig. 7); yellow region on lower surface of HW with black stripe across middle (Fig. 25) *jenia*
- 2. Dorsal margin of sacculus with triangular lobe near middle; apical part of valve nearly straight *otasa*
- Dorsal margin of sacculus not lobed; apical part of valve distinctly curved 3
- 3. Sclerotized dorsal edge of juxta v-shaped, the convergent sides nearly straight in outline (Fig. 17); uncus with lateral outline slightly concave, straight, or evenly convex (Figs. 12–17) *franclemonti*
- Sclerotized dorsal edge of juxta with two rounded lobes protruded posteriorly, in outline forming two rounded lips separated by a distinct notch (Fig. 19); uncus with lateral lobes 4
- 4. Uncus with distal lateral outline evenly convex (similar to Figs. 9–10) *tusora*
- Uncus with greatly enlarged lateral lobes (Figs. 11, 19) *franclemontoides*, n. sp.

PHYLOGENETIC RELATIONSHIPS

There are few characters shared among the five species of the *A. franclemonti* group that permit phylogenetic analysis relative to an outgroup consisting of all other species of *Aucula*. Five informative characters were observed as follows, the state occurring in the outgroup scored 0:

- Character 1.* Lateral lobes of uncus: 0, present; 1, absent.
- Character 2.* Lateroventral outline of apical half of valve: 0, straight; 1, concave, smoothly curved; 2, concave, deeply angled.
- Character 3.* Distinct, rounded lobes on dorsal edge of juxta: 0, absent; 1, present.
- Character 4.* Ventral outline of valve at distal end of sacculus: 0, smoothly curved; 1, sharply angled.
- Character 5.* Length of free, apical extension of valve: 0, apex of valve not conspicuously elongated; 1, apex of valve elongated and constricted.

Characters were distributed as follows, with the number of each character followed by its state in parentheses: *A. jenia*, 1(0), 2(0), 3(0), 4(1), 5(1); *A. otasa*, 1(1), 2(2), 3(1), 4(1), 5(1); *A. franclemonti*, 1(1), 2(1), 3(0), 4(1), 5(1); *A. franclemontoides*, 1(1), 2(2), 3(1), 4(1), 5(1); *A. tusora*, 1(1), 2(1), 3(1), 4(1), 5(1); other *Aucula* species (outgroup), 1(0), 2(0), 3(0), 4(0), 5(0). Characters autapomorphic for single species were not considered, such as small body size and a notch in the dorsal margin of sacculus in *A. otasa*, the black HW stripe in *A. jenia*, huge uncal lobes in *A. franclemontoides*, and a relatively short apical elongation of the valve in *A. tusora*.

A phylogenetic analysis produced a minimally supported but fully resolved hypothesis of relationship. All possible phylogenetic trees (105) were examined with respect to the above five characters, and a single tree of minimum length (Fig. 21) was found without invoking hypotheses of homoplasy (Consistency = 1.00). East Andean species from Ecuador, Peru, and Bolivia (*A. tusora*, *A. otasa*, and *A. franclemontoides*) are hypothesized to form a monophyletic subgroup based on distinctive lobing of the juxta. This subgroup and *A. franclemonti* form a monophyletic group supported by two synapomorphies, uncal lobes and an inwardly curved or angled ventral margin along the outer half of the valve.

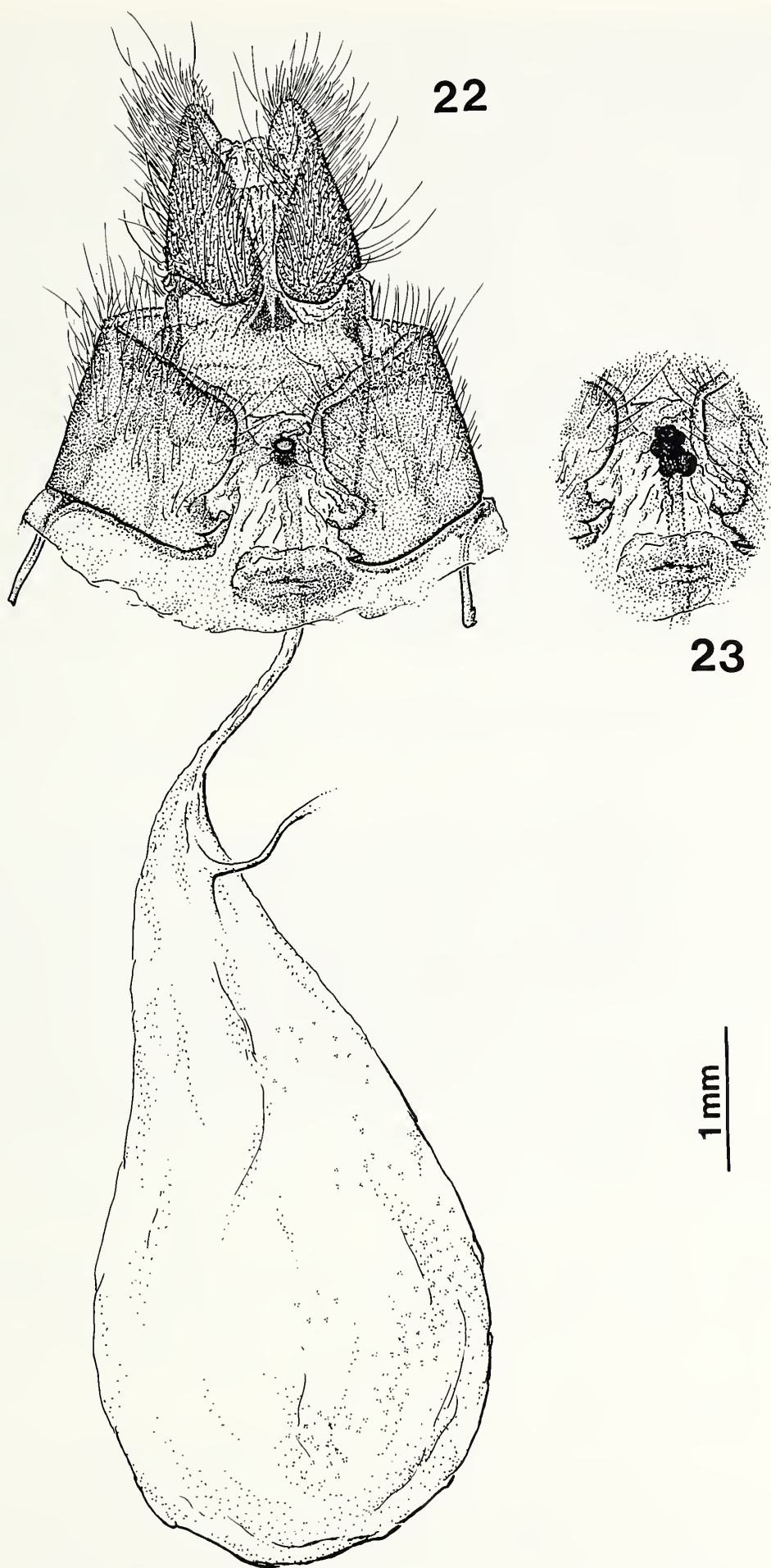
The monophyly of the *A. franclemonti* group is supported by two derived characters, apical elongation of the valves and a sharply angled ventral margin at the distal end of the sacculus. On the other hand, there is no evidence that other species of *Aucula* form a monophyletic group, and genitalic features suggest that the immediate sister-lineage to the *A. franclemonti* group may be one including *Aucula byla* Todd and Poole. There is also serious question whether the genus *Aucula* is monophyletic as treated by Todd and Poole (1981), because diagnostic features currently used to define the genus, such as wing shape, coloration, and the absence of a median process of the sacculus, are not convincingly apomorphic at the level of Agaristinae.

DESCRIPTION OF THE ADULT FEMALE OF *AUCULA FRANCLEMONTI*

Todd and Poole only briefly described females of *Aucula* and their genitalia. A more complete description of female *A. franclemonti* is given here based on three specimens, two mated females caught in the field (one is the female parent of CMNH Culture 83-186), and a single virgin female eclosing in the laboratory (CMNH Culture 83-351).

General. Maculation, color, and shape as in males with the following differences: size slightly larger than males (FWL = 27–28 mm); costa of forewing slightly but distinctly angled just beyond middle; apical segment of labial palp more than twice as long as wide (length and width subequal in males).

Female genitalia. Figure 22. Lobes of papillae anales subtriangular due to slight elongation of posterior dorsal angle; lobes sparsely setose, more densely so near posterior margins; posterior apophyses compressed and widened near base, cylindrical anteriorly, subequal in length to papillae anales; Tergum 8 unmodified; anterior apophyses slightly shorter than posterior apophyses; ostium bursae small, circular, sclerotized, located in membranous protuberance between ventral edges of Tergum 8; ductus bursae straight, slender, membranous, sclerotized only at extreme base by ostium bursae; corpus bursae membranous, ovoid, tapered smoothly into ductus bursae; anterior enlargement of corpus bursae (fundus bursae) without signa but with



Figs. 22–23. Female genitalia of *Aucula franclemonti* (Genitalia slide: Rawlins 859 (CMNH)).
22. Ventral view without sphragis. 23. Detail of ostial region with sphragis in position.



Figs. 24–25. Ventral view of *Aucula* species. 24. Female of *A. franclemonti* (CMNH Culture No. 83-351) during reflex immobilization following a slight disturbance. 25. Ventral view of *A. jenia*, male; forewing length 23 mm; Ecuador, Chimborazo (CMNH).

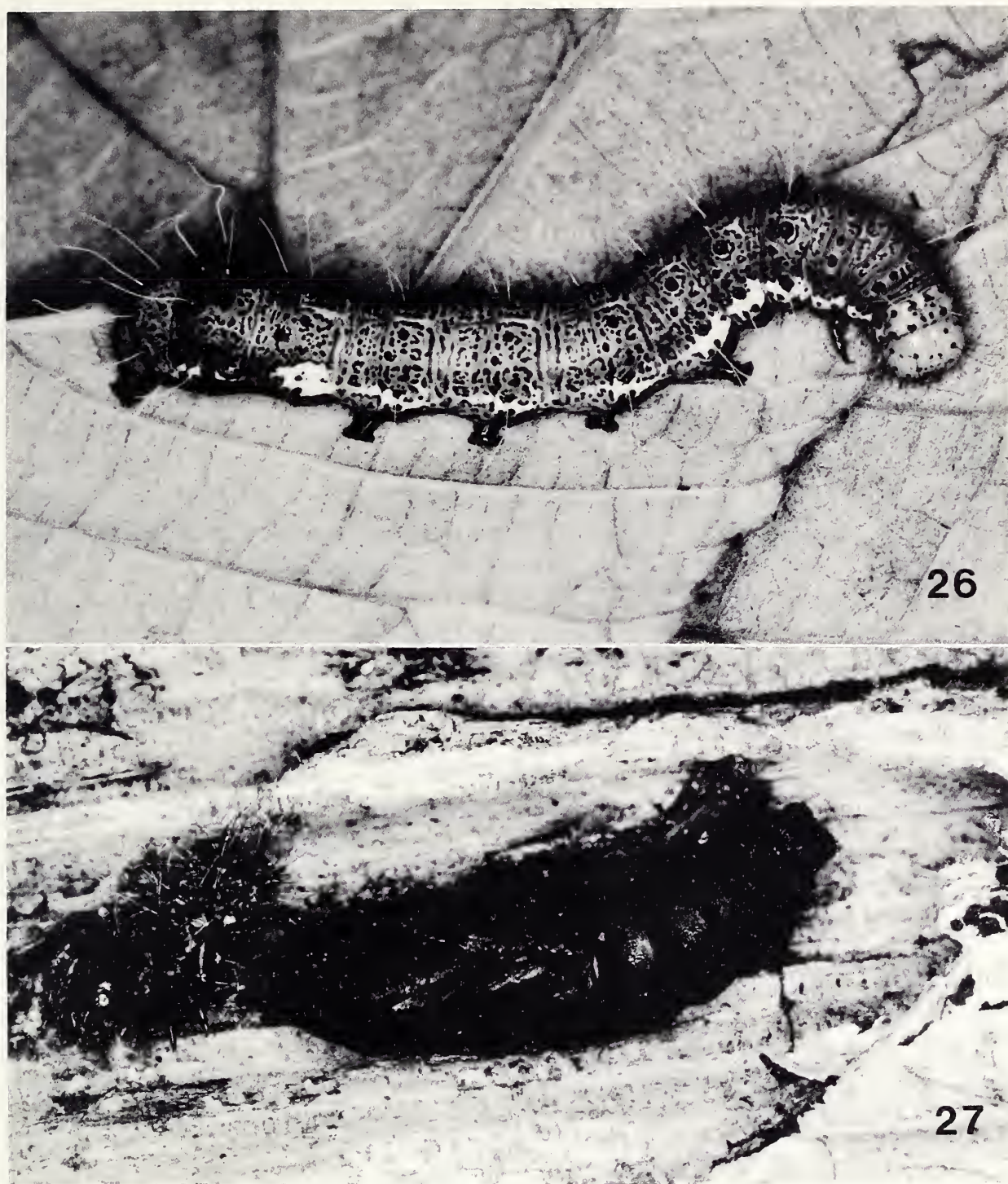
sparsely scattered acanthae; small medial zone of irregular sclerotization anterior to ostium bursae, reflexed under Sternum 7; posterior margin of Sternum 7 sclerotized, broadly concave. Mated female without discernable internal spermatophore; plug of amorphous sclerotized material in ostium bursae (Fig. 23), extended inward along short sclerotized base of ductus bursae, and outward over protuberance encircling ostium.

Discussion. The external female genitalia are structurally correlated in size and shape with the male genitalia. The small ostium and adjacent sclerotized portion of the ductus bursae match precisely in diameter and length the permanently everted and strongly sclerotized endophalli of males.

A sclerotized plug was present in the ostia bursarum of both mated females, and absent in the single female known to be virgin by virtue of its having eclosed in isolation. The chitinous nature of this copulatory obstruction suggests that it is probably homologous to the collum of the unmodified noctuid spermatophore. Its presence in both mated females available for study, and its absence in a virgin female, suggests that it is functioning as a sphragis preventing multiple matings. I am not aware of sphragides elsewhere in the Noctuidae.

LIFE HISTORY NOTES ON *AUCULA FRANCLEMONTI*

A female of *A. franclemonti* was collected on 5 July 1983 at the same Ecuadorian locality as the series of 23 males discussed above. A search was made for likely foodplants in the Onagraceae, Vitaceae, and Portulacaceae in anticipation of obtaining another gravid female. Another female was taken on the night of July 11. When



Figs. 26–27. Immature stages of *Aucula franclemonti* (CMNH Culture No. 83-351). 26. Last larval instar resting on under surface of leaves of foodplant, *Vitis tiliifolia*. 27. Pupa exposed in pupal chamber formed by boring in soft wood; pupal position reversed from that found in nature.

placed in a small container with leaves of a wild grape (*Vitis*, Vitaceae), it deposited 28 eggs by the morning of July 12. These hatched after an incubation period of slightly more than four days. Five eggs and five first instars were preserved (CMNH Culture 83-186), and the remaining larvae began feeding at once on the dorsal surface of wild grape leaves. First instar larvae remained relatively immobile on the leaves while feeding, but when disturbed moved about rapidly as “semiloopers” with prolegs advancing the length of two or more segments at each step (multisegmental loco-

motion). Detailed developmental observations were not made, but three late third instars were preserved on July 26, and two last larval instars (fifth) were preserved on August 3, 18 days after hatching. The last three instars moved by advancing the prolegs a single segment per step without semilooping (unisegmental locomotion), and fed by biting leaf edges.

During the rapid development of this isofemale culture, larvae were sought in the field on foliage of the same species of *Vitis*. During the night of 26 July 1983, a last instar larva was found feeding by Mark Smyers (Fig. 26). On July 31, the larva began boring into rotting wood, constructing a pupation chamber which was rendered observable by carefully splitting the piece of wood into which it had bored. The chamber was completed by August 1, and the prepupa remained inactive for four days, pupating on August 5 (Fig. 27). The pupal chamber was transported back to a laboratory at the University of Texas, Austin. By rare good fortune, eclosion of a female moth was directly observed on 11 September 1983 at 10:00 hours CST. The freshly eclosed moth climbed up to an elevated position in the laboratory enclosure and remained motionless for nearly 40 minutes before expansion of the wings. When disturbed, this virgin female defended itself by reflex immobilization with the wings appressed stiffly above the abdomen and the abdomen expanded and strongly curved under the thorax (Fig. 24), similar to the behavior of wild-caught males and other aposematic Lepidoptera, including a diversity of sympatric Arctiidae (Watson, 1975).

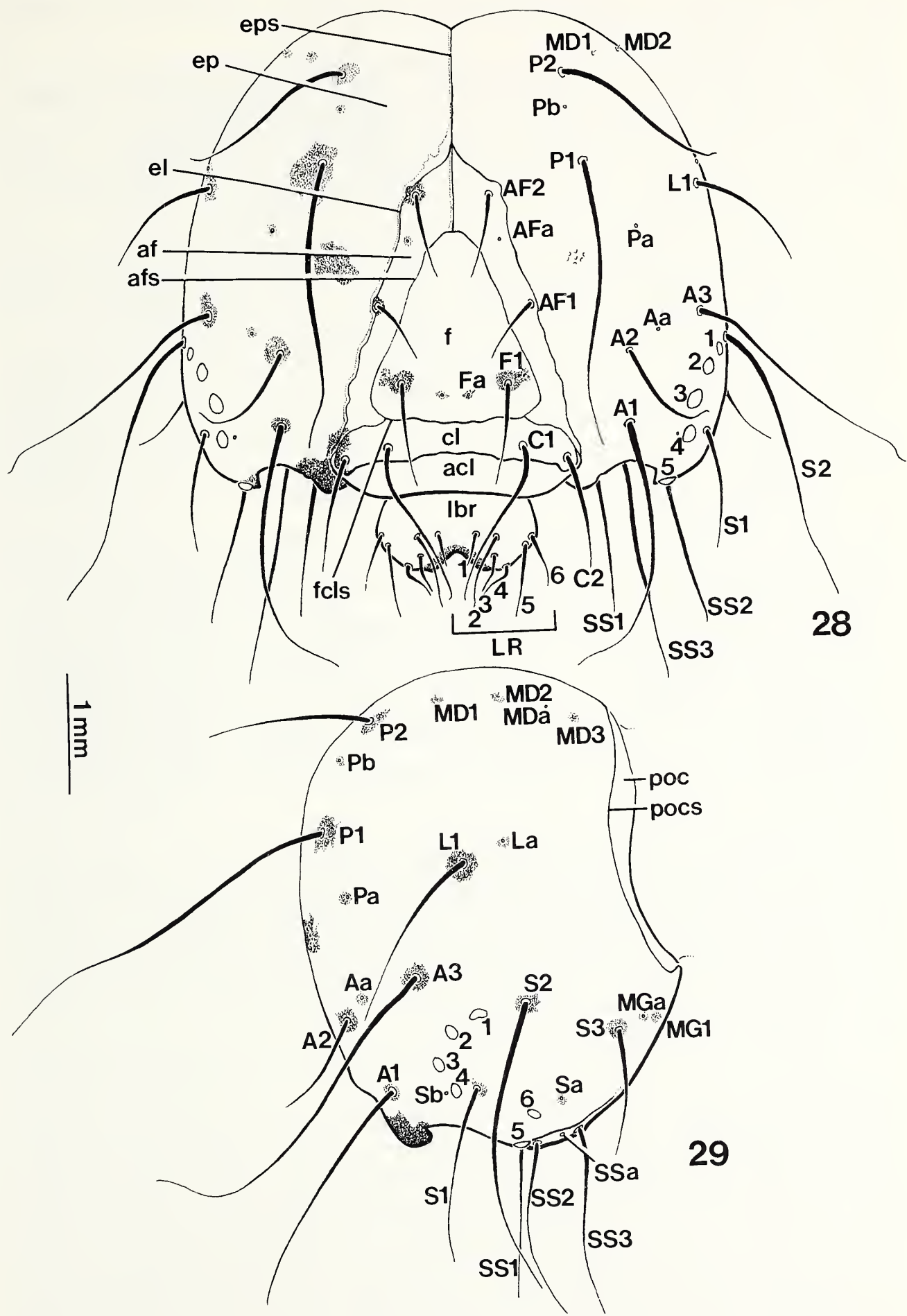
Foodplant: *Vitis tiliifolia* Humb. & Bonpl. ex. Roem. & Schultes; voucher specimen in herbarium of Carnegie Museum, Thompson and Rawlins No. 811, collected 10 July 1983. Determination by Michael O. Moore, 1990, The University of Georgia.

The immature stages of *A. franclemonti* are described briefly below.

Egg: Deposited singly or in clumps of 2–3 against major veins on underside of leaf of foodplant, partially or completely inserted under lanate pubescence. Pale yellow when laid, turning reddish brown prior to hatch. Egg slightly variable in size and shape, moderately flattened; diameter, 0.96–1.09 mm; height, 0.60–0.74 mm. Microsculpture consisting of 22–25 vertical costulae only slightly raised above outline of egg; all vertical costulae begin near outer edge of flattened base of egg, but only half extend to micropylar rosette, the other half evanescent at about $\frac{7}{8}$ the distance to rosette; long and short vertical costulae alternating; vertical costulae connected by diffuse transverse costulae, separating columns of 10–13 indistinct areoles. Micro-

→

Figs. 28–29. Chaetotaxy of the head of last instar larva of *Aucula franclemonti*. 28. Dorsal view of head. 29. Lateral view of head. Symbols used: A1–A3, anterior setae; Aa, anterior pore; acl, anteclypeus; af, adfrontal sclerite; AF1–AF2, adfrontal setae; AFa, adfrontal pore; afs, adfrontal suture (=lateral adfrontal suture); cl, clypeus (=postclypeus of authors); CL1–CL2, clypeal setae; el, ecdysial line; ep, epicranium; eps, epicranial suture (=coronal suture or medial adfrontal suture); f, front; F1, frontal seta; Fa, frontal pore; fcls, frontoclypeal suture; L1, lateral seta; La, lateral pore; lbr, labrum; LR1–LR6, labral setae; MD1–MD3, dorsal proprioceptor setae; MDa, dorsal pore; MG1, genal proprioceptor seta; MGa, genal pore; P1–P2, posterior setae; Pa–Pb, posterior pores of head; poc, postocciput; pocs, postoccipital suture; S1–S3, stemmatal setae; Sa–Sb, posterior stemmatal pores; SS1–SS3, substemmatal setae; SSa, substemmatal pore.



pylar rosette less than 0.10 mm in diameter, surrounded by a slight depression joining upper ends of vertical costulae.

First instar: Length, 2.8–3.2 mm; width of head, 0.52 mm. Head yellowish brown, body pale grayish white with long white setae arising from contrasting brown pinaculæ. Tactile setae as in last instar with the following exceptions: only one SV seta present on A1 and A7, two SV setae present on A2; five coxal setae (DC1–DC2 missing, Figs. 36–37). Prolegs on A5 and A6 subequal, those on A4 slightly smaller, those on A3 still smaller.

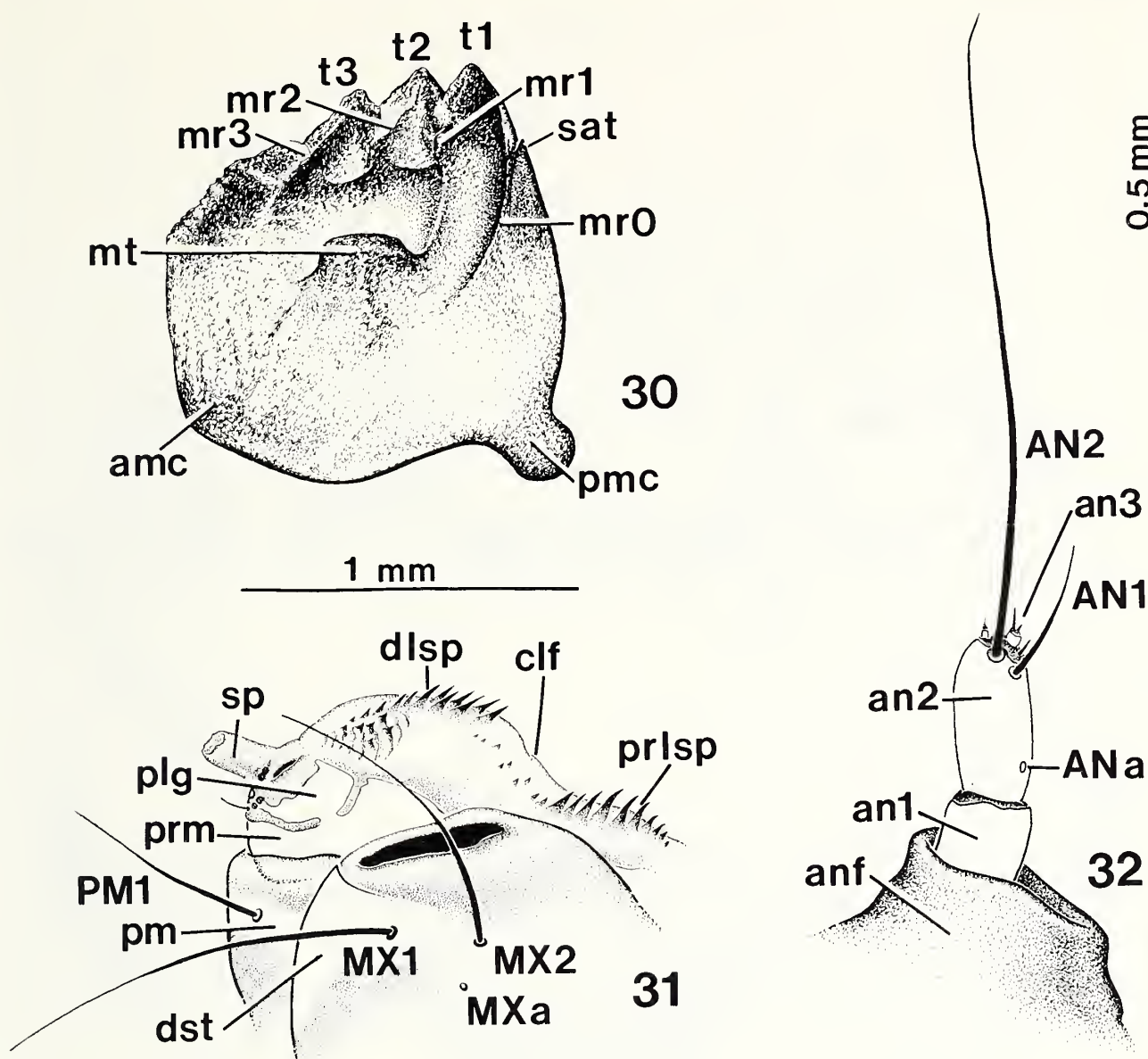
Intermediate instars: Head yellow, with setal bases minutely but contrastingly dark brown. Body color pale reddish gray, densely spotted with dark spots vaguely forming broken transverse stripes. Two SV setae on A7, the anteriormost seta (SV2) much smaller than the posterior and on a separate pinaculum.

Last instar: Length, 48 mm; head width, 4.5 mm; width of mandible, 1.16 mm. Head blocky, strongly hypognathous, width greater than prothorax. Body elongate, enlarged gradually posteriorly, distinctly swollen on Ab8; most setae long, conspicuous, erect (especially on segment Ab8), set in distinct, slightly elevated pinaculæ which are enlarged dorsally (especially dorsal pinaculæ on segment Ab8). Detailed chaetotaxy and external morphology presented below.

Head pale brownish yellow, bases of setae brownish black. Thorax and abdomen with ground color light gray tinted with olivaceous to yellowish brown on middle of segments; pattern of dark gray to black spots, forming irregular transverse bands on posterior portion of segments; transverse pattern less distinct anteriorly on each segment; segments T2 to Ab9 with large blotches of white laterally, most extensive on sides of Ab7 in subdorsal and lateral regions; ventral region on all segments pale yellowish white, contrasting with adjacent subventral color. Prothoracic and anal shields concolorous with head; thoracic legs brownish yellow on ventral and lateral surfaces, darker brown on dorsal surface; subventral pinaculum above prolegs yellowish brown dorsally, darker brown ventrally; spiracles black; most setae pale gray to white.

Pupa (terminology follows Mosher, 1916): Length, 22 mm. Pupa very dark reddish brown, dull in lustre due to strong microsculpture which is finely spinulose dorsally. Labial palpus visible externally; base of maxilla extended laterally to sculptured eyepiece; prothoracic femur not visible; mesothoracic leg not extended anteriorly to sculptured eyepiece (externally not contiguous with eyepiece); terga 3 and 4 separated by flexible cuticle, not fused; cremaster truncate, with flattened lateral processes bearing reduced setae along posterior margins.

Discussion: Although the egg does not differ in a distinctive way from many other non-agaristine noctuids, the larval and pupal stages of *A. franclemonti* are characteristic of those found in a diverse representation of other agaristines that I have reared and studied in detail (e.g., *Alypia octomaculata* (Fabricius), *Brephos nyassana* (Bartel), *Chelonomorpha formosana* Miyake, *Euscirrhopterus gloveri* Grote and Robinson, *Eudryas grata* (Fabricius), *Eudryas unio* (Hübner), *Mimeusemia vilemani* Hampson, *Psychomorpha epimenis* (Drury), *Tuerta chrysochlora* Walker, *Xerociris wilsonii* (Grote)). In particular, mature larvae are characterized by pale, hypognathous head capsules with setal insertions often accentuated with dark spots; body segments with contrasting transverse patterns of 1–8 bands, sometimes broken into spots (*Aucula*) or obscured by a dark ground (*Xerociris*), often with patches of orange or white laterally. These larval generalizations hold for many species described in some



Figs. 30–32. Mouthparts of last instar larva of *Aucula franclemonti*. 30. Medial surface of left mandible. 31. Left lateral view of hypopharyngeal complex, labial and maxillary palp; removed. 32. Left antenna. Symbols used: amc, anterior mandibular condyle; AN1–AN2, setae of an2; an1–an3, antennal segments; ANa, pore of an2; anf, antennifer; clf, transverse cleft of hypopharynx; dlsp, distolateral spinules; dst, dististipes (=palpifer of authors); mr0, outer mandibular ridge; mr1–mr3, inner mandibular ridges; mt, inner tooth; MX1–MX2, setae of maxillary stipes; MXa, pore of basistipes; plg, palpiger (=stipes labii of Crumb (1929)); pm, postmentum; PM1, postmental seta; pmc, posterior mandibular condyle; prlsp, proximolateral spinules; prm, prementum; sat, subapical cleft; t1–t3, apical teeth.

detail by Gardner (1946, 1948; *Aegocera venulia* (Cramer), *Sarbanissa albifascia* (Walker)), by Crumb (1956; *Alypia langtonii* Couper, *Alypia ridingsii* Grote, *Androloma maccullochii* (Kirby) (but body pattern longitudinal), *Eudryas brevipennis* Stretch, *Euscirrhopterus cosyra* (Druce)), those figured by Sugi (1987; *Asteropetes noctuina* (Butler), *Chelonomorpha japana* Motschulsky, *Maikona jezoensis* Matsumura, *Sarbanissa subflava* (Moore), *S. venusta* (Leech)) and those figured by Common (1990; *Agarista agricola* (Donovan), *Argyrolepidia subaspersa* (Walker), *Cruria donowani* (Boisduval), *Comocrus behri* (Angas), *Periscepta polysticta* (Butler), *Phalaenoides tristifica* (Hübner)). Of all agaristines known to this author, the immature stages of *A. franclemonti* most closely resemble those of *Mimeusemia vilemani* from Taiwan.

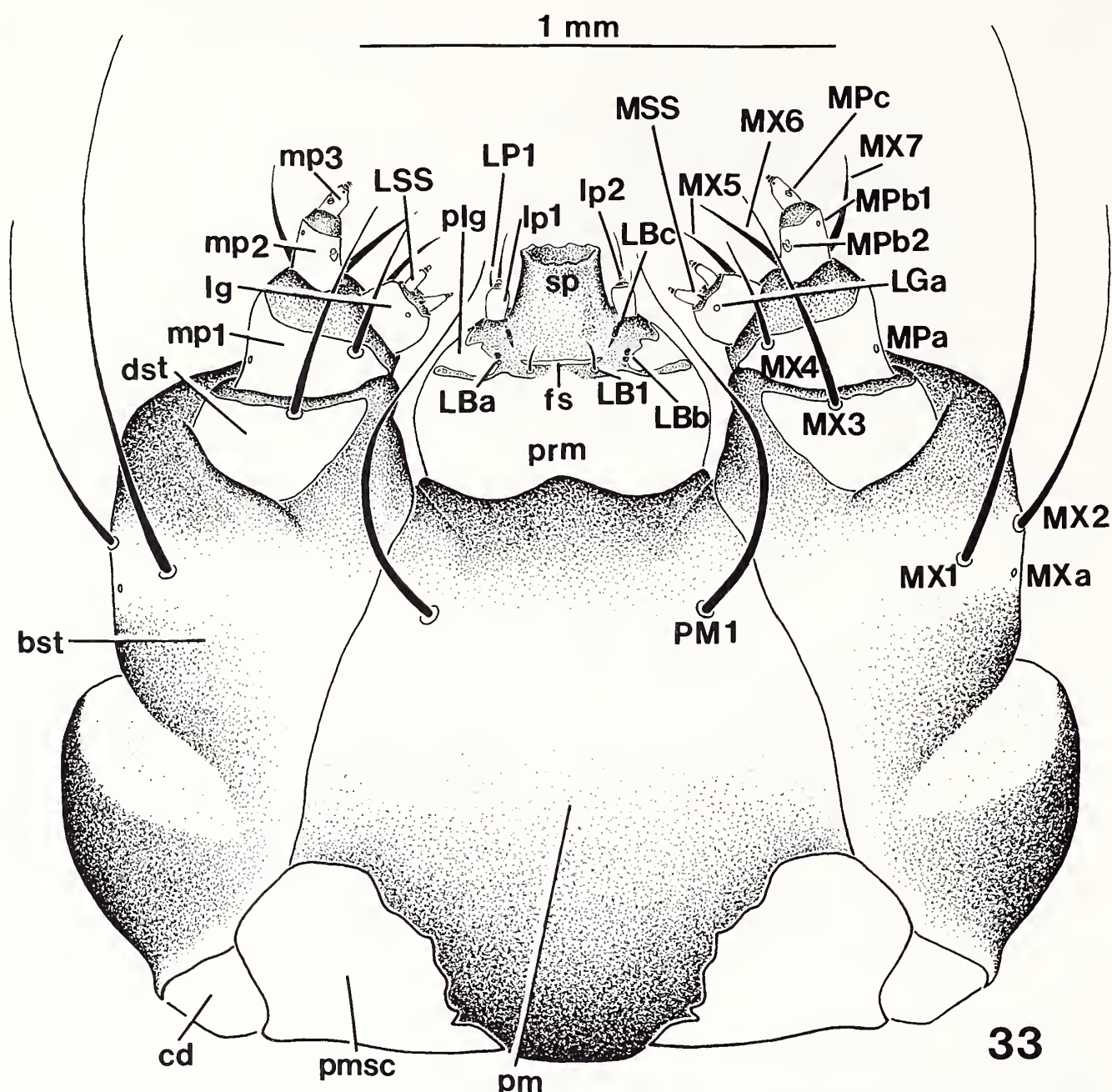
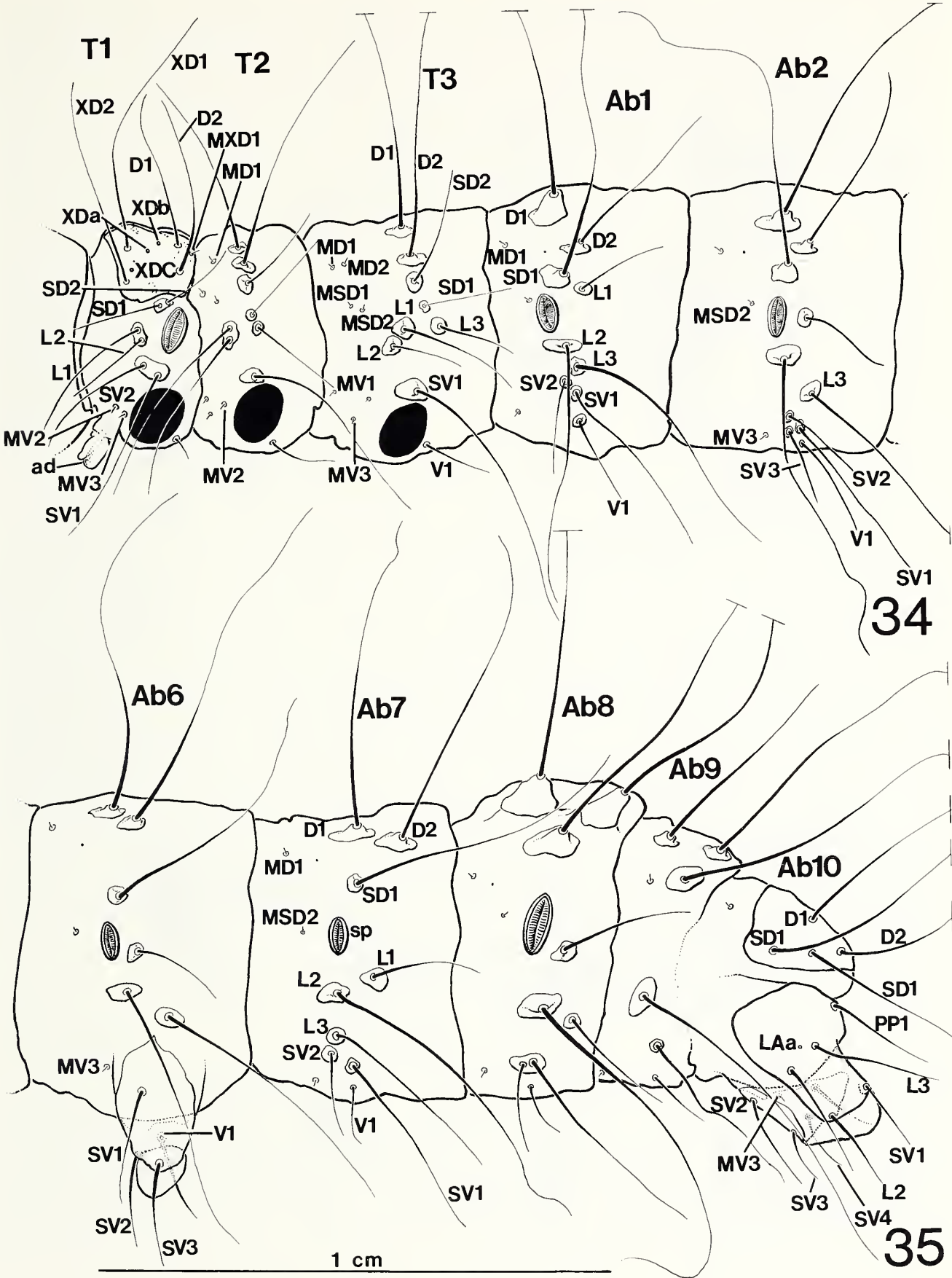
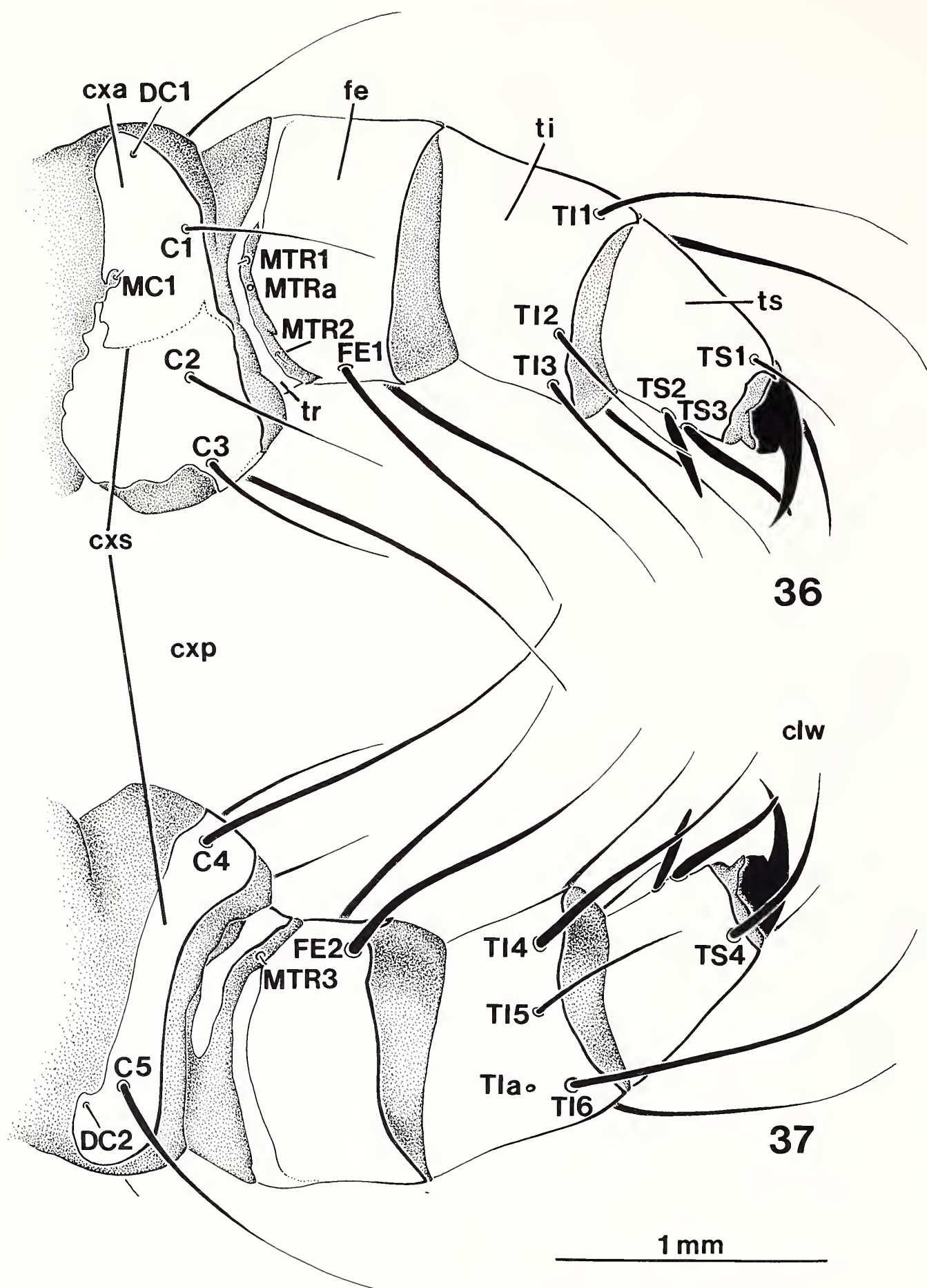


Fig. 33. Maxillolabial complex of last instar larva of *Aucula franclemonti* (semischematic). Symbols used: bst, basistipes; cd, cardo; dst, dististipes; fs, fusiliger; LB1, stipular seta of labium; LBa–LBc, pores of palpiger; lg, laciniogalea; LGa, pore of laciniogalea (=Mxe of Gerasimov); LP1, apical seta of lp1; lp1, basal segment of labial palpus; lp2, distal segment of labial palpus; LSS, lateral sensillum styloconicum of laciniogalea; mp1–mp3, segments of maxillary palpus; MPa, pore of basal segment of maxillary palpus (=Mxd of Gerasimov); MPb1, lateral pore of mp2 (=Mxf of Gerasimov); MPb2, medial sensillum of mp2; MPc, pore of mp3 (=Mxj of Gerasimov (1952)); =SD of Grimes and Neunzig (1986a); MSS, medial sensillum styloconicum of laciniogalea; MX1–MX3, setae of maxillary stipes; MX4, seta of first segment of maxillary palpus; MX5–MX7, apical setae of maxilla (=STIII–STI of Grimes and Neunzig, 1986b)); MXa, pore of basistipes; plg, palpiger; pm, postmentum; PM1, postmental seta; pmsc, posterior sclerotization of postmentum; prm, prementum; sp, spinneret.

→
Figs. 34–35. Chaetotaxy of the body segments of last larval instar of *Aucula franclemonti* (semischematic views). 34. Left side of thorax and first two abdominal segments. 35. Left side of abdominal segments 6–10. Symbols used (broken outlines indicate features hidden from view by other structures): Ab1–Ab10, abdominal segments; ad, adenosma (ventral cervical



gland); D1-D2, dorsal setae; L1-L3, lateral setae; LAa, lateral pore of Ab10; MD1, dorsal proprioceptor seta; MSD1-MSD2, subdorsal proprioceptor setae; MV1-MV3, ventral proprioceptor setae; MXD1, posterior proprioceptor seta of T1; PP1, paraproct seta; SD1-SD2, subdorsal setae; spr, spiracle; SV1-SV4, subventral setae; T1-T3, thoracic segments; V1, ventral seta; XD1-XD2, anterior dorsal setae of T1; XDa-XDc, anterodorsal pores of T1.



Figs. 36–37. Chaetotaxy of the prothoracic leg of last instar larva of *Aucula franclemonti*. 36. Anterior view of left prothoracic leg. 37. Posterior view of left prothoracic leg. Symbols used: C1, seta of anterior coxal sclerite; C2–C5, setae of posterior coxal sclerite; clw, claw of pretarsus; cxa, anterior sclerite of coxa; exp, posterior sclerite of coxa; cxs, coxal suture; DC1–

The pupation chamber and pupa of *A. franclemonti* are also very similar to those of agaristine species I have studied (see list above). Pupation occurs in chambers bored in soft wood. Pupae characteristically have heavy microsculpture, are often spinulose dorsally, and the truncate cremaster bears flattened lateral flanges with setae greatly reduced or absent. The labial palpi are visible, the prothoracic femora are not, and the mesothoracic leg is not contiguous with the eyepiece. Terga 3 and 4 are not fused but are closely joined by flexible intersegmental cuticle.

The vitaceous host of *A. franclemonti* is expected, as most of the known foodplants for agaristine species worldwide are in the Vitaceae, including Leeaceae (Rhamnales), and the remainder in the following unrelated families of plants: Dilleniaceae (Dilleniales); Lauraceae (Laurales); Onagraceae (Myrtales); Haloragaceae (Haloragales); Portulacaceae, Nyctaginaceae and Cactaceae (Caryophyllales); Loranthaceae (Santalales); Boraginaceae (Lamiales); Rubiaceae (Rubiales); Araceae (Arales); Smilacaceae and Dioscoreaceae (Liliales).

CHAETOTAXY OF THE MATURE LARVA OF *AUCULA FRANCLEMONTI*

Chaetotaxy and general morphological features are presented in considerable detail in Figure 28–37. No previous author has presented exhaustively the chaetotaxy of an entire larval noctuoid, although a consistently applied terminology for most setae has emerged in recent years as best summarized by Stehr (1987). Current setal nomenclature for Lepidoptera larvae results from a long and confusing history of comparative study including Fracker (1915), Schierbeek (1917), Hinton (1946), Gerasimov (1952), and Hasenfuss (1963). Descriptive work with noctuoid larvae has become increasingly refined since early work by Ripley (1923) and Crumb (1929), through comprehensive, regional treatments by Gardner (1946, 1948), Crumb (1956), Beck (1960), and Godfrey (1972, 1987), to an exceptionally detailed and well-illustrated work by Miller (1991) who illustrated the partial chaetotaxy of the agaristine *Alypia octomaculata*. Beck (1960) and Godfrey (1972) provide nomenclature for the hypopharyngeal complex, and Godfrey (1972) supplies a general rationale for description of the mandible, similar in principle to that proposed by Gerasimov (1952). A review of chaetotaxy for abdominal segment 10 was given by Stehr (1987), but locations for the various setae were not clearly illustrated and application of his terminology remains problematic for lateral and subventral setae of the last abdominal segment.

Two systems, the maxillolabial complex and the thoracic legs, have not been consistently illustrated or labelled in larval descriptions, although Gerasimov (1952) offered a system naming most setae. Grimes and Neunzig (1986a, 1986b) provided a clear nomenclature for apical sensillae of the terminal segment of the maxillary palpus and the laciniogaleae, but did not offer terminology for more basal setae or sensillae of the maxilla. The setae of the thoracic legs were labelled in part by

←

DC2, dorsal subprimary seta of coxa; fe, femur; FE1–FE2, femoral setae; MC1, proprioceptor seta of anterior coxal sclerite; MTR1–MTR3, proprioceptor setae of trochanter; MTRa, antero-dorsal pore of trochanter; ti, tibia; T11–T16, tibial setae; tr, trochanter; ts, tarsus; TS1–TS4, tarsal setae.

Gerasimov (1952), but his system was not closely or consistently followed by recent treatments (Nielsen and Kristensen, 1989; Miller, 1991).

Chaetotaxal nomenclature adopted here follows the Hinton system (1946) as summarized by Stehr (1987) but agrees with Singh and Goel's (1987) interpretation of subdorsal abdominal setae. Nomenclature of setae and pores on the prothorax follows Hinton (1946), not Hasenfuss (1963), and the names of those on abdominal segment 10 follows Stehr (1987). Terminology for the mandibles follows Gerasimov (1952) and Godfrey (1972); that for the hypopharyngeal complex follows Godfrey (1972). Names for setae and pores of the antenna, maxilla, and labium follow Gerasimov (1952) where possible, conflicting with Grimes and Neunzig (1986b) only with respect to three setae (sensillae) of the laciniogalea. Finally nomenclature for the setae and pores of the thoracic legs follows Gerasimov (1952) in part, differing from the systems proposed by Miller (1991) and Nielsen and Kristensen (1989).

Names and symbols for setae newly applied in this paper are in agreement with general principles of a system first introduced by Hinton (1946). His nomenclature based on relative morphological position may be rendered useful, informative, and straightforward by attention to synonymy, homonymy, and priority of usage by earlier authors. Numbering of setae within groups follows general trends and facilitates rapid and accurate recognition of setae: ontogenetic appearance, anterior to posterior, dorsal to ventral, medial to lateral, and sequential continuity around circular or cylindrical structures. Where possible, symbols for setae and pores are chosen as mnemonic abbreviations of the names they represent. Abbreviations for a few head setae have been changed from those of Hinton to avoid homonymy with those on other body parts, but the L and MD setae of the head and body are still homonymous. Finally, symbols for setae and pores are entirely upper case followed by numbers for setae and lower case letters for pores; symbols for sutures, sclerites, and other structures and regions are lower case with the exception of traditional symbols for segments, T1–T3, Ab1–Ab10.

Head: Figures 28–29. Only a single substemmatal pore and a single genal proprioceptor seta on each side of head; six labral setae (here symbolized LR1–LR6 following a peripheral sequence, medial to lateral, around each labral lobe) but no obvious labral pores; three stout but otherwise unmodified epipharyngeal setae.

Antenna: Figure 32.

Mandible: Figure 30. Three distinct apical teeth are subtended by three inner ridges, the first ridge as numbered here originates from the posterior side of a truncate, inner mandibular tooth; a tiny subapical cleft present where outer (posterior) mandibular ridge joins distal margin of mandible.

Maxilla: Figure 33. Nomenclature for apical setae follows Gerasimov (1952), MX5–MX7, equalling STIII to STI of Grimes and Neunzig (1986b); pore MPc is the same as Mxj of Gerasimov (1952) and the sensillum digitiformium (SD) of Grimes and Neunzig (1986a).

Hypopharyngeal complex: Figure 31. Proximolateral spinules long, well developed; medial surface of hypopharynx smooth; transverse cleft indistinct, not sharply incised.

Labium: Figure 31, 33. Nomenclature for divisions of the mentum follows Snodgrass (1935). Spinneret almost as wide as long, membranous, broadly tubular.

Thorax: Figure 34. Two SV setae on segment T1, and one SV seta on segments T2–T3. Seta L2 on segment T1 and seta SD1 on segments T1–T3 are very attenuated,

straight sensillae borne in darkly pigmented pits with densely microtrichiated walls (tonosensillae: Rawlins, 1984). These setae are receptors of airborne sound in noctodontid larvae (Tautz and Markl, 1978).

Abdomen: Figures 34–35. Four SV setae present on segment Ab10, three SV setae present on segments A2–A6, two SV setae present on segments Ab1, Ab7, and Ab8, and one SV seta present on segment Ab9. Seta L1 posterior to spiracle on segments Ab1–Ab6 and Ab8; below spiracle on segment Ab7; spiracles subequal on segments Ab1–Ab7, enlarged on Ab8; seta SD1 on segment Ab9 normal in size and shape, not a tonosensillum.

Thoracic legs: (Figs. 36–37). Coxa divided into anterior and posterior sclerites by an anteroventral coxal suture extended as coxal condyle articulating with trochanter; five primary coxal setae present, one (C1) on anterior coxal sclerite, and four (C2–C5) on posterior coxal sclerite, numbered in continuous sequence around coxa; one small (or proprioceptor) seta on basal edge of anterior coxal sclerite near coxal suture (MC1); one reduced, subprimary seta basal to seta C1 (DC1), and similar reduced seta (DC2) basal to seta C5. Three proprioceptor setae in membranous gap between trochanter and base of femur, numbered sequentially around segment from a relatively anterodorsal position dorsal to coxal suture (MTR1), to an anteroventral position below coxal suture (MTR2), to a posteroventral position (MTR3); a pore (MTRa) situated between seta MTR1 and point opposite coxal suture. Femur without pores; with two setae, anterior (FE1) and posterior (FE2). Tibia with a single posterodorsal pore (T1a) and six setae encircling apex, numbered as Gerasimov (1952) in a continual sequence: anterodorsal (T11), anterolateral (T12), anteroventral (T13), posteroventral (T14), posterolateral (T15), posterodorsal (T16). Tarsus with four setae, numbered as the tibia: anterodorsal (TS1, a small seta), anteroventral (TS2), posteroventral (TS3, just distad of TS2), and posterodorsal (TS4, larger than TS1); setae TS2 and TS3 stout, slightly flattened and bladellike.

Discussion. Three features of the chaetotaxy of *Aucula franclemonti* deserve special emphasis: the presence of two SV setae on segment Ab1, two SV setae on segment Ab7, and a normal, non-attenuated seta SD1 on segment Ab9. The number of SV setae on the first abdominal segment has been an important character in the classification of Lepidoptera larvae, noctuoid and otherwise. The significance of three SV setae on Ab1 was stressed by Gardner (1946, 1948) and by Crumb (1956) in recognizing several subfamilies of Noctuidae (all Catocalinae *sensu lato*, Herminiinae, Bagisarininae, and Hypeninae) as well as several species of Plusiinae, Acontiinae *sensu lato* (nearctic species of *Lithacodia* and *Eublemma*), and Amphipyryinae (species variously placed by authors in *Perigea*, *Platysenta*, *Condica*, and *Leuconycta*). All agaristine larvae examined in this study had two SV setae on Ab1, the usual condition for the “trifid” subfamilies.

The presence of two SV setae on segment Ab7 appears to be a diagnostic feature of most Agaristinae, and it was utilized in a key to subfamilies for North American species by Crumb (1956). I have examined larvae of species worldwide (listed above), and all have two SV setae on Ab7 except those of *Psychomorpha epimenis*, a North American species placed in the Agaristinae without comment by Crumb (1956). Only a single SV seta was found on Ab7 in noctuid taxa of controversial affinities, including those known to have additional SV setae on thoracic or other abdominal segments: *Litoprosopus futilis* (Grote and Robinson), *Diaphone eumela* (Stoll), *Xanthopastis*

timais (Cramer), *Diphthera festiva* (Fabricius). The second SV seta on Ab7 is absent in first instar larvae of Agaristinae, and its presence in subsequent instars appears to be an excellent synapomorphy of most species in the subfamily.

Two SV setae have been observed on Ab7 of the very similar larvae of New World *Bagisara* species (*B. rectifascia* (Grote) and *B. repanda* (Fabricius)) and Old World *Xanthodes transversa* Guenée. The former genus is placed by most authors in Acontiinae, and the latter in Chloephorinae by Poole (1989), but both may best be treated as a distinct taxon, Bagisarinae (or Bagisarini of the Acontiinae), as established by Crumb (1956). The additional subventral seta on Ab7 in both subfamilies is always smaller than the usual subventral seta (SV1), anterior to it, and never on the same pinaculum.

In agaristines the additional seta is always distinctly dorsal to the level of SV1, in a position spatially identical to that of setae SV2 on the first and second abdominal segments, and is therefore labelled SV2. In most agaristines, SV2 on Ab7 is slightly dorsal to SV1, but in *T. chrysochlora* SV2 is positioned so far dorsad that its pinaculum is fused with that of seta L3.

In bagisarines, the additional subventral seta on Ab7 is far ventrad of SV1, and may be almost as close to the ventral midline as seta V1 in a position spatially similar to that of SV3 on the second abdominal segment. This seta in bagisarines should be labelled SV3, and is not considered homologous to SV2 in agaristines.

Aucula franclemonti and all other Agaristinae examined lack a tonosensillum on segment Ab9. As on the thorax, the seta that is modified into a tonosensillum is SD1. The presence of this tonosensillum in many "trifid" noctuids (Abrostolini, Amphipyridae, Cuculliinae, Glottulini, Hadeninae, Heliothinae, Noctuinae, Stiriini), but not in other Noctuoidea, suggests that it may be synapomorphic for a major lineage of Noctuidae. A comprehensive, worldwide survey of this setal modification has not been undertaken, but its absence in Agaristinae does not support their inclusion in an extensive "trifid" lineage bearing the modified seta.

ACKNOWLEDGMENTS

Special appreciation is due the following for helping with this study: M. A. Klingler for his detailed illustrations; G. L. Godfrey, C. W. Young and R. L. Davidson for review of the manuscript; M. A. Daman and W. A. Zanol for assistance in specimen and manuscript preparation; M. Smyers for exceptional success in caterpillar-hunting in 1983; I. Kitching and M. Honey for facilitating study at The Natural History Museum, London; S. A. Thompson for foodplant vouchering and obtaining an authoritative foodplant identification from M. O. Moore; G. Onore for logistical help in Ecuador. Last, but not least, I thank J. G. Franclemont for so generously sharing with me his truly insatiable passion for moths and their larvae.

LITERATURE CITED

- Beck, H. 1960. Die larvalsystematik der Eulen (Noctuidae). Abhandl. Larvalsyst. Ins. (Akademie-Verlag, Berlin) 4:1–406.
Common, I. F. B. 1990. Moths of Australia. E. J. Brill, New York.
Crumb, S. E. 1929. Tobacco cutworms. USDA Tech. Bull. 88:1–179.
Crumb, S. E. 1956. The larvae of the Phalaenidae. USDA Tech. Bull. 1135:1–356.

- Fracker, S. B. 1915. The classification of lepidopterous larvae. Illinois Biol. Monogr. 2:1–169.
- Gardner, J. C. M. 1946. On larvae of the Noctuidae (Lepidoptera)—II. Trans. Roy. Ent. Soc. Lond. 97:237–252.
- Gardner, J. C. M. 1948. On larvae of the Noctuidae (Lepidoptera)—VI. Trans. Roy. Ent. Soc. Lond. 9:291–318.
- Gerasimov, A. M. 1952. Caterpillars, Part 1. Fauna SSSR: Insects—Lepidoptera 1(2):1–338. Zool. Inst. Acad. Nauk SSSR, New Series, No. 56. [In Russian]
- Godfrey, G. L. 1972. A review and reclassification of larvae of the subfamily Hadeninae (Lepidoptera: Noctuidae) of America north of Mexico. USDA Tech. Bull. 1450:1–265.
- Godfrey, G. L. 1987. Noctuidae (Noctuoidea). Pages 549–578 in: F. W. Stehr (ed.), Immature Insects. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Grimes, L. R. and H. H. Neunzig. 1986a. Morphological survey of the maxillae in last stage larvae of the suborder Ditrysia (Lepidoptera): palpi. Ann. Ent. Soc. Am. 79:491–509.
- Grimes, L. R. and H. H. Neunzig. 1986b. Morphological survey of the maxillae in last-stage larvae of the suborder Ditrysia (Lepidoptera): mesal lobes (laciniogaleae). Ann. Ent. Soc. Am. 79:510–526.
- Hasenfuss, I. 1963. Eine vergleichen-morphologische Analyse der regulären Borstenmuster der Lepidopterenlarven. Studien zur Methodik der vergleichenden Morphologie der Borstenmuster und zur phylogenetischen Deutung der Abwandlungen der regulären Borstenmuster der Lepidopterenlarven. Z. Morph. Okol. Tiere 52:197–364.
- Hinton, H. E. 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy. Ent. Soc. Lond. 97:1–37.
- Kiriakoff, S. G. 1977. Lepidoptera Noctuiiformes, Agaristidae. III. (American Genera). Das Tierreich 99:1–82.
- Miller, J. S. 1991. Cladistics and classification of the Notodontidae (Lepidoptera: Noctuoidea) based on larval and adult morphology. Bull. Am. Mus. Nat. Hist. 204:1–230.
- Mosher, E. 1916. A classification of the Lepidoptera based on characters of the pupa. Bull. Illinois State Lab. Nat. Hist. 12(2):14–159, plates 19–27.
- Nielsen, E. S. and N. P. Kristensen. 1989. Primitive Ghost Moths. Morphology and taxonomy of the Australian genus *Fraus* Walker (Lepidoptera: Hepialidae s. lat.). Monographs on Australian Lepidoptera 1:1–206.
- Poole, R. W. 1989. Lepidopterorum Catalogus (New Series). Fascicle 118. Noctuidae, Part 1. E. J. Brill/Flora and Fauna Publications, New York, pp. 1–500.
- Rawlins, J. E. 1984. Mycophagy in Lepidoptera. Pages 382–483 in: Q. Wheeler and M. Blackwell (eds.), Fungus-Insect Relationships. Perspectives in Ecology and Evolution. Columbia University Press, New York.
- Ripley, L. B. 1923. The external morphology and postembryology of noctuid larvae. Illinois Biol. Monogr. 8:1–169.
- Schierbeek, A. 1917. On the Setal Pattern of Caterpillars and Pupae. E. J. Brill, Leiden.
- Singh, G. P. and S. C. Goel. 1987. Body chaetotaxy of three noctuid caterpillars. Deutsch. Ent. Zeit. 34:373–381.
- Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co., New York.
- Stehr, F. W. 1987. Immature Insects. Kendall/Hunt Publishing Co., Dubuque, Iowa.
- Sugi, S. (ed.). 1987. Larvae of Larger Moths in Japan. Kodansha Co. Ltd., Tokyo. [In Japanese with English summary]
- Tautz, J. and H. Markl. 1978. Caterpillars detect flying wasps by hairs sensitive to airborne vibration. Behavioral Ecol. Sociobiol. 4:101–110.
- Todd, E. L. and R. W. Poole. 1981. A revision of the agaristid genus *Aucula* Walker (Lepidoptera: Noctuidae). J. Lep. Soc. 35:194–215.

- Watson, A. 1975. A reclassification of the Arctiidae and Ctenuchidae formerly placed in the thyretid genus *Automolis* Hübner (Lepidoptera) with notes on warning coloration and sound. Bull. British Mus. Nat. Hist. (Ent.), Suppl. 4:1-104, 34 plates.

Received 31 July 1991; accepted 22 Nov 1991.